



Revision of the Lichen Genus *Stereocaulon* (Stereocaulaceae, Ascomycota) in South Korea

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ABSTRACT

Lichen genus *Stereocaulon* (Schreb.) Hoffm. is distributed throughout the world. Although 15 *Stereocaulon* species have been recorded in Korea, no detailed taxonomic or revisionary research has been conducted for nearly two decades. In this study, we collected 260 putative *Stereocaulon* spp. samples and identified the species based on morphological, chemical, and molecular characteristics. From the collected samples, 10 species of *Stereocaulon* were identified, nine of which had already been reported, although this was the first report for the tenth, *S. octomerellum* Hue, in Korea. General characteristics of *Stereocaulon* spp. include coralloid phyllocladia and tubercular cephalodia; however, the specimen first collected in Korea was a rare species with tomentum on the pseudopodetia. The specimen of *S. octomerellum* is characterized by the presence of a primary thallus, granule to short coralloid phyllocladia, and pseudopodetia up to 1 cm in size, with tubercular cephalodia. To determine the phylogeny of the specimens, we compared the ITS sequences of ribosomal DNA and the β -tubulin gene sequences. Phylogenetic analysis showed that the Korean *Stereocaulon* species were monophyletic and placed in the previous phylogenetic classification. Species of *S. intermedium* and *S. exutum*, however, were polyphyletic, and are morphologically variable and widespread species. Overall, we present here detailed morphological and chemical descriptions of each species identified and a revised key of all known *Stereocaulon* species in South Korea.

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1. Introduction

The lichen genus *Stereocaulon* Hoffm. is a cosmopolitan genus consisting of approximately 125 species of common fruticose lichens [1,2]. *Stereocaulon* spp. are generally composed of a primary thallus, pseudopodetia, phyllocladia, cephalodia, and apothecia, although only some species have soredia and tomentum. Primary thalli of *Stereocaulon* spp. are short lived or persistent, consisting of tiny white granules or squamules, and pseudopodetia are erect or decumbent. Cephalodia are chlorococcoid (*Trebouxia*) or blue-green (*Nostoc* or *Stigonema*), and are attached to the primary thallus or pseudopodia, which can be spherical to botryose and sacculate [2,3]. Phyllocladia are classified into coralloid, granular, squamulose, and peltate types [3]. During growth of these lichens, cephalodia appear at an early stage and persist on the basal part of the pseudopodetia, and pseudopodetia arise from the primary thallus by elongation of the thalline tissue as areolae or verrucae [3,4].

A worldwide key, a conspectus, and a classification of the genus *Stereocaulon* based on morphology, chemistry, and ontogeny were produced by Lamb [3,5,6]. Alongside morphological classification, molecular analysis of the genus *Stereocaulon* has been studied using the internal transcribed spacer (ITS) regions of ribosomal DNA and partial β -tubulin gene regions [4]. Using these two molecular markers, Högnabba analyzed the phylogenetic status of 49 out of 125 known taxa [4]. This study revealed that *Stereocaulon* was polyphyletic and the morphological classification of *Stereocaulon*, suggesting morphological analysis may not be exactly in accord with molecular analysis [4].

To date, 15 *Stereocaulon* species have been reported in South Korea [7]. Before 1950, Japanese lichenologists, Sato and Ueda, reported three *Stereocaulon* species, *S. coralloides*, *S. paschale*, and *S. wrightii* [8,9]. Later, Kim reported five different *Stereocaulon* species, including *S. apocalypticum*, *S. curtatum*, *S. japonicum*, *S. paschale*, and *S. wrightii*.

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[10]. Park described nine more species in South Korea, including *S. commixtum*, *S. dendroides*, *S. exutum*, *S. intermedium*, *S. nigrum*, *S. octomerum*, *S. sorediiferum*, *S. verruculigerum*, and *S. vesuvianum* [11]. In 2002, Kasiwadani additionally reported the presence of *S. pileatum* in Korea [12]. Although a number of studies have been conducted on the genus *Stereocaulon* in Korea, none has conducted molecular analysis.

In the present study, the taxonomy of *Stereocaulon* species in Korea is revised based on morphological and chemical characteristics and molecular phylogenetic analysis. A key to all known *Stereocaulon* species in Korean is also presented.

2. Materials and methods

2.1. Morphological examination

Samples of the genus *Stereocaulon* were collected in South Korea from 2003 to 2016 (Figure 1). The specimens were deposited at the herbarium of KoLRI (Korea Lichen Research Institute). Descriptions of the external morphology were based on air-dried materials observed under a Nikon SMZ-645 dissecting microscope (Nikon Corp., Tokyo, Japan) and an Olympus BX-50 compound microscope (Olympus, Tokyo, Japan) was used to study the anatomy of ascocarps. Color reaction tests were conducted on phyllocladia and pseudopodetia to check for secondary metabolites. (K = 10% aqueous KOH solution, P = 5% alcoholic *p*-phenylenediamine solution) [13]. Thin-layer chromatography (TLC) was performed in Solvent A (toluene:dioxin:acetic acid = 180:45:5) and solvent C (toluene:acetic acid = 85:15) [14].

2.2. DNA extraction and PCR amplification

Total DNA was extracted directly from the lichen thalli using the DNeasy Plant Mini Kit (QIAGEN, Dusseldorf, Germany). The partial 18 s rRNA-ITS1-5.8 s rRNA-ITS2-partial 28 s rRNA region was amplified with universal primers ITS1F [15], ITS4 [16], or LR5 [17]. PCR amplification was carried out using a Takara JP/TP600 PCR machine (Takara Bio Inc., Kusatsu, Japan) under the following conditions: initial cycle of 5 min at 94 °C, followed by 30 cycles of 30 seconds at 94 °C, 30 seconds at 55 °C, 10 min at 72 °C, and then finally 10 min at 72 °C. The partial β-tubulin sequence was amplified with Bt3-LM and Bt10-LM [18] or Bt-PJS-F1(5'-GCCTCTGGCAAATATGT-3') and Bt-PJS-R1(5'-AATTCTGGCACGGTGACC-3').

β-tubulin samples were prepared in the same way as ITS samples. The PCR reaction of β-tubulin was carried out in a 2720 thermal cycler PCR machine

(Applied Biosystems, Singapore, Singapore) under the following conditions: initial cycle of 5 min at 94 °C, followed by 30 cycles of 30 seconds at 94 °C, 30 seconds at 55 °C initially, and then 52 °C for the remaining cycles, 1 min at 72 °C, and finally 72 °C for 5 min [4].

PCR products were purified using a PCR quick-spin PCR Product Purification Kit (INTRON Biotechnology, Inc., seoul, South Korea) and then sent to Genotech Cooperation (Daejeon, Korea) for sequencing.

2.3. Sequence alignments and phylogenetic analysis

The sequences were manually edited and assembled using CodonCode Aligner (CodonCode Corporation, Dedham, MA) and BIOEDIT 7.0.9 [19]. All the sequences generated in this study and sequences retrieved from GenBank were initially aligned using Clustal W ver. 1.83 [20]. Two lichen species, *Cladonia ahtii* (AF45327) and *C. rangiformis* (AF455172) were used as outgroups. Phylogenetic analysis was conducted using the maximum parsimony (MP) method and neighbor joining (NJ) in MEGA version 6.0 software [21]. Reliability of the inferred tree was tested by 1000 bootstrap replications of the MP and NJ tree. Kimura two-parameter model was used for the analysis of the NJ method.

3. Results and discussion

3.1. Taxonomy and distribution of the genus *Stereocaulon* in Korea

The genus *Stereocaulon* was collected all over South Korea along Baekdudaegan from the truce line to Jeju Island (Figure 1). Taxonomic identification was carried out as per Lamb's taxonomic keys [6]. The taxonomic characteristics of the genus *Stereocaulon* in South Korea are described at the end of this report.

A total of 260 *Stereocaulon* specimens were collected from eight different sampling sites (Figure 1; marked in gray) and 59.2% of them were collected on Jeju Island. Using morphological and chemical analysis, we identified 10 *Stereocaulon* species: *S. dendroides*, *S. exutum*, *S. japonicum*, *S. intermedium*, *S. nigrum*, *S. octomerellum*, *S. pileatum*, *S. sorediiferum*, *S. verruculigerum*, and *S. vesuvianum* var. *nodosum*. Nine of these 10 species have already been reported in Korea in previous studies [10]; however, this is the first report for *S. octomerellum*.

The distribution of the 10 species identified is shown in Figure 2. *S. japonicum* (34% of total 260 specimens collected) was the most common *Stereocaulon* species, distributed throughout

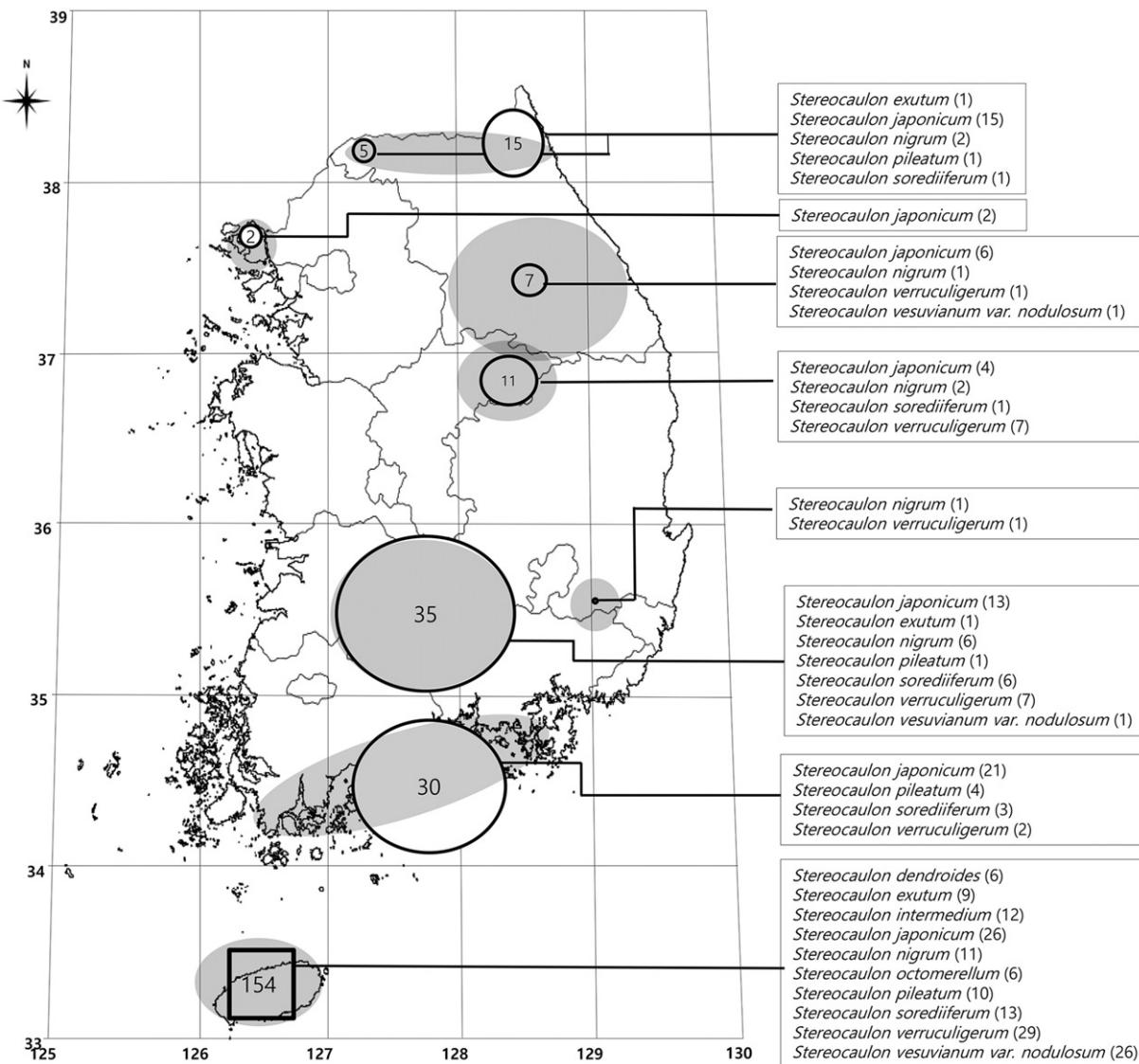


Figure 1. Collection map of *Stereocaulon* specimens during 2003–2016 in South Korea.

South Korea at all sampling sites (Figures 2(A) and 3(A)). The second most common was *S. verruculigerum*, with 47 specimens (18%) in South Korea (Figures 2(B) and 3(B)). Twenty-eight specimens of *S. vesuvianum* var. *nodulosum* (11%) (Figures 2(C) and 3(C)), 24 of *S. sorediiferum* (9%) (Figures 2(D) and 3(D)), 23 of *S. nigrum* (9%) (Figures 2(E) and 3(E)), and 16 of *S. pileatum* (6%) (Figures 2(F) and 3(F)) were distributed in various regions. *S. intermedium* (5%) (Figures 2(G) and 3(G)), *S. exutum* (4%) (Figures 2(H) and 3(H)), and *S. dendroides* (2%) (Figures 2(I) and 3(I)) were mainly observed in Jeju Island.

Six specimens of *S. octomerellum* (2%), which had not yet been reported in South Korea, were collected from Mt. Halla in Jeju Island (Figures 2(J) and 3(J)). This species is characterized by pseudopodetia less than 1 cm in size, a short coraloid or granule form of phyllocladia, and colorless hypothecium (Figure 3(K)). The *S. octomerellum* specimens collected were very similar to *S. verruculigerum* and were found to contain lobaric acid. The main

substances of Korean *Stereocaulon* are stictic acid and lobaric acid, and nine of the 10 species identified in this study were classified as producers of these two substances, whereas *S. dendroides* produces porphyrilic acid.

Previously, *Stereocaulon* was collected mainly from Mt. Halla, Mt. Jiri, and Mt. Sorak [11,12]. In addition, more studies on *Stereocaulon* have been conducted in Japan and China than in South Korea. In Japan, *Stereocaulon* was classified by Asahina and 33 species and 3 subspecies were reported [22–25]. In China, *Stereocaulon* was classified by Huang and 44 species were reported [26,27]. Also in Japan and China, *Stereocaulon* species have been classified on the basis of morphology and secondary metabolite chemistry, but not using molecular biology approaches.

3.2. Phylogenetic analysis

To perform molecular phylogenetic analysis, we randomly selected two representative specimens for

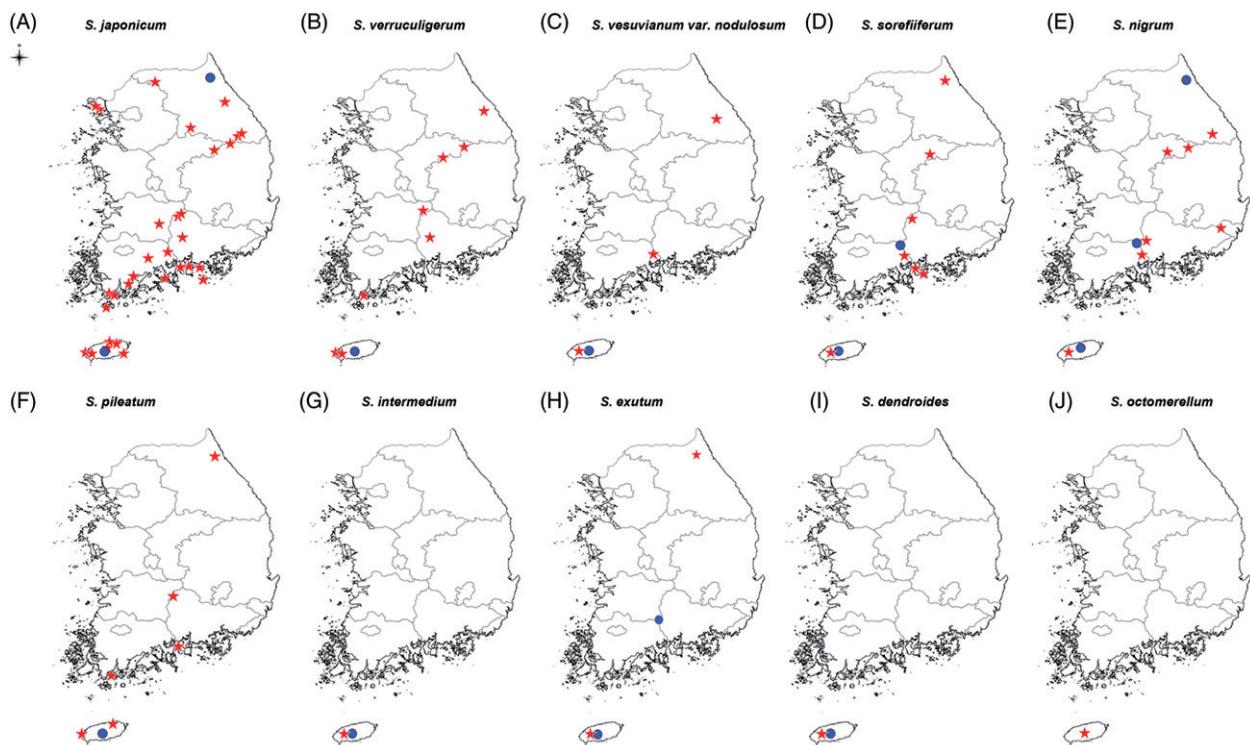


Figure 2. Distribution of *Stereocaulon* species in South Korea. Circle indicates *Stereocaulon* species that was also found in a previous study. Stars indicates samples collected in this study. (A) *S. japonicum*; (B) *S. verruculigerum*; (C) *S. vesuvianum* var. *nodosum*; (D) *S. soreiiferum*; (E) *S. nigrum*; (F) *S. pileatum*; (G) *S. intermedium*; (H) *S. exutum*; (I) *S. dendroides*; (J) *S. octomerellum*.

each of the 10 *Stereocaulon* species identified. Two general molecular sequences for the genus *Stereocaulon*, ITS1–5.8s rRNA–ITS2 regions, and protein-coding gene β -tubulin, were used for the analysis [28]. Length variation of ITS1 and ITS2 was 225 to 238 bp and 93 to 154 bp, respectively. All sequences from 5.8 s rRNA were of identical length. For β -tubulin, all intron lengths were the same and the lengths of exon 5 and exon 6 were also the same for all species, except exon 5 of *S. exutum* and *S. soreiiferum*, which were shorter than that of the other species. All generated sequences were deposited in NCBI and the accession numbers are listed in Table 1 and Supplementary data S1.

For phylogenetic analysis, we retrieved sequences of both the ITS regions and the β -tubulin gene from 58 *Stereocaulon* species obtained in a previous study [4]. We merged the sequences of both ITS regions and the β -tubulin gene that showed 1338 characters containing 746 conserved characters and 583 variable characters. The MP analyses were applied to generate a phylogenetic tree as previously described [4]. One of the most parsimonious trees is shown in Figure 4. We also constructed an NJ tree in Supplementary data S2 for comparison with the MP tree. Both phylogenetic trees had the same structure, and the interspecific relationship was also the same.

Stereocaulon spp. in South Korea analyzed in this study was found to be polyphyletic with a low support value, as in previous studies [4]. Unlike the

previous analyses, however, *S. soreiiferum* did not exist as a monophyletic clade at the base of the tree but was also grouped with subsection Aciculisporae. This result was probably resulted from the use of only β -tubulin sequences in previous studies [4].

Stereocaulon japonicum was grouped in the same clade with the reference *S. japonicum* sequence that we used in this study (Figure 4). However, in a previous study, the reference *S. japonicum* samples were separated into two different clades, suggesting that it is a polymorphic species. We observed that *S. verruculigerum* was in the same clade as *S. japonicum* with a well-supported bootstrap value. However, in a previous study, *S. verruculigerum* was placed in a different clade from *S. japonicum*, although it has been reported that *S. verruculigerum* is highly similar to *S. japonicum* in their morphology and both species are generally classified by the presence or the absence of stictic acid and lobaric acid [6].

Stereocaulon dendroides was newly sequenced in this study. From previous studies, it was known that *S. dendroides* and *S. pendulum* contain the same chemicals [6]. Interestingly, we observed that our *S. dendroides* species clustered with *S. pendulum*.

Our two Korean *S. exutum* samples did not belong to the same clade; one (Hur 130031) of the two specimens was in the same clade as the reference *S. exutum* (Inoue 28958) but the other was not. Two *S. nigrum* samples were grouped in the same

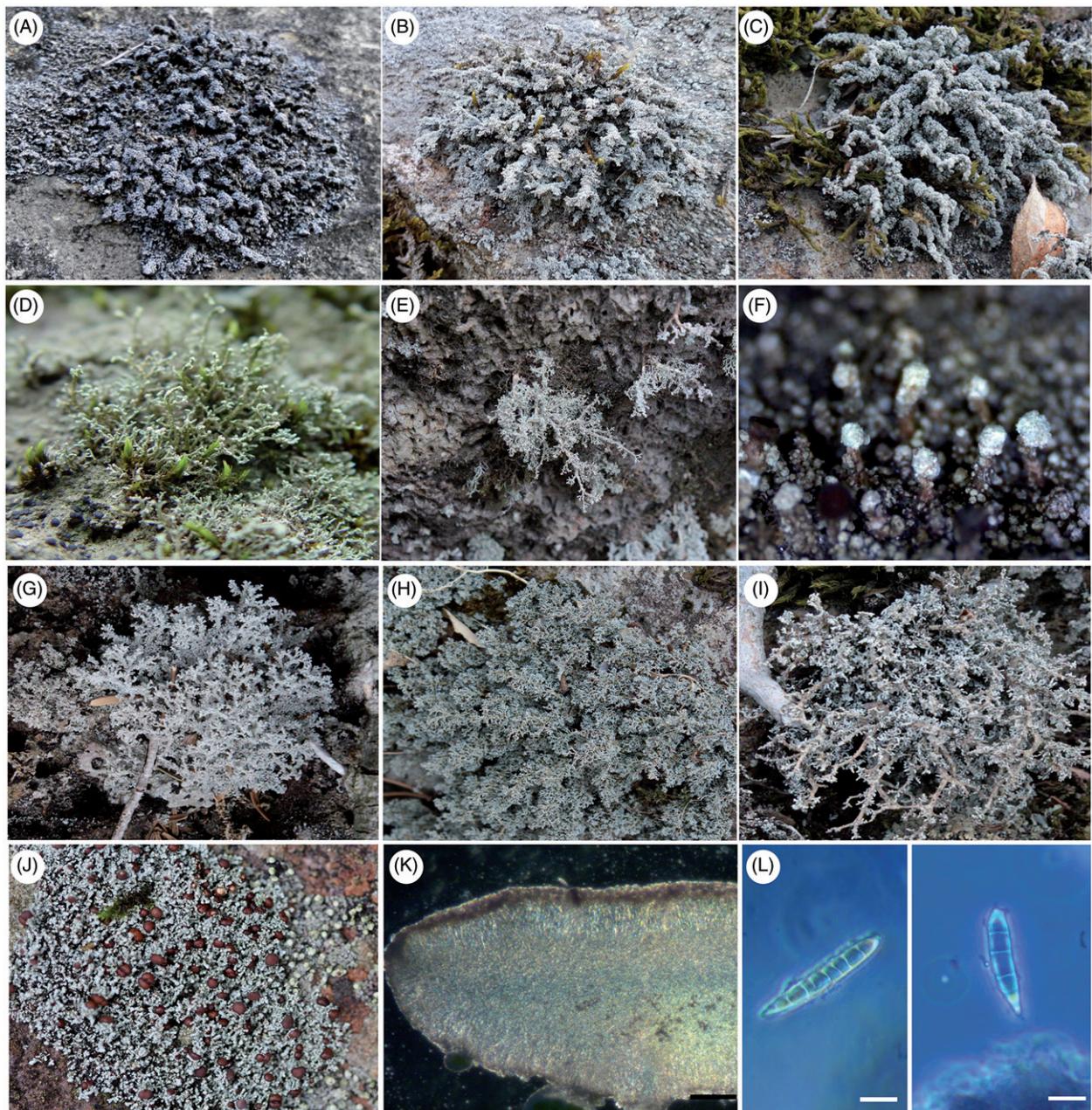


Figure 3. Habit of the *Stereocaulon* species. (A) *S. japonicum* Hur130006; (B) *S. verruculigerum* Hur141605; (C) *S. vesuvianum* var. *nodulosum* Hur130060; (D) *S. sorexiferum* Hur040639; (E) *S. nigrum* Hur130045; (F) *S. pileatum* Hur121814; (G) *S. intermedium* Hur130044; (H) *S. exutum* Hur130030; (I) *S. dendroides* Hur130059; (J) *S. octomerellum* Hur121094; (K) Hypothecium color of *S. octomerellum*; (L) Spore type and septation of *S. octomerellum* (Scale bars: K = 100 μm , L = 10 μm).

clade with *S. exutum*, as it have a highly similar morphology to *S. exutum* (Figure 4).

The β -tubulin sequence from *S. pileatum* and the ITS sequence from *S. octomerellum* were newly sequenced and analyzed in this study. The phylogenetic analysis showed that these two species were in the same clade with a well-supported bootstrap value. It is known that these two species have pseudopodetia less than 1 cm in size. In previous studies, *S. pileatum* and *S. verruculigerum* were grouped in the same clade using only the ITS nucleotide sequence. As a result of using two markers, *S. pileatum* was grouped in the clades with other lichens

that were morphologically similar, such as *S. octomerellum*.

As previously reported, *S. vesuvianum* var. *nodulosum* was grouped together with *S. arcticum*. The two species are very similar in morphology and the only difference is the presence or the absence of *Stigonema* and *Nostoc* in the cephalodia [29].

We observed that our *S. intermedium* specimens were separated from the reference *S. intermedium* in the phylogenetic tree (Figure 4). Although previous studies have referred to this species as a single lineage, our results indicate that our *S. intermedium* is in a different clade, with a well-supported bootstrap

Table 1. Specimens used in molecular phylogenetic analysis.

Name of species	GenBank No.		
	ITS	β -tubulin	Collection
<i>Cladonia ahti</i>	AF453275	AF458486	Brazil, Ahti & Eliasaro 57582 (H) ^a
<i>C. rangiformis</i>	AF455172	AF458522	Sweden, Stenroos 5125 (TUR)
<i>Stereocaulon alpestre</i>	DQ396833	DQ396976	Iceland, Baldursdóttir s. n. (H)
<i>S. alpinum</i>	DQ396898	DQ396978	Italy, Hyvönen 6877a (TUR)
<i>S. alpinum</i>	DQ396900	DQ396979	Argentina, Stenroos 5499 (TUR)
<i>S. alpinum</i>	DQ396903	DQ396982	Argentina, Stenroos 5523 (TUR)
<i>S. alpinum</i>	DQ396915	DQ396993	Argentina, Stenroos 5459 (TUR)
<i>S. alpinum</i>	DQ396917	DQ396995	Argentina, Stenroos 5496 (TUR)
<i>S. alpinum</i>	DQ396960	DQ397032	Austria, Feuerer 60471a (HBG)
<i>S. arcticum</i>	DQ396953	DQ397027	Svalbard, Inoue 28418 (TUR)
<i>S. arcticum</i>	DQ396956	DQ397029	Svalbard, Inoue 28229 (TUR)
<i>S. azoreum</i>	DQ396966	DQ397036	Madeira, Krebs 5175 (B)
<i>S. botrysom</i>	DQ396952	DQ397026	Svalbard, Inoue 28228 (TUR)
<i>S. coniophyllum</i>	DQ396936	DQ397011	China, Obermayer 8634 sorediate (GZU)
<i>S. coniophyllum</i>	DQ396937	DQ397012	China, Obermayer 8635 sorediate (GZU)
<i>S. coniophyllum</i>	DQ396939	DQ397014	China, Obermayer 8354 (GZU)
<i>S. coniophyllum</i>	DQ396943	DQ397016	China, Obermayer 8643 (GZU)
<i>S. corticatum</i>	DQ396904	DQ396983	Argentina, Stenroos 5403 (TUR)
<i>S. corticatum</i>	DQ396905	DQ396984	Argentina, Stenroos 5545 (TUR)
<i>S. curtatum</i>	DQ396949	DQ397023	Japan, Inoue 28955 (TUR)
<i>S. dendroides</i> ^b	KY660026	KY827015	Korea, Hur 141476 (KoLRI)
<i>S. dendroides</i>	KP324743	KY827016	Korea, Hur 141477 (KoLRI)
<i>S. depreautii</i>	DQ396947	DQ397021	Japan, Inoue 28664 (TUR)
<i>S. evolutum</i>	DQ396922	DQ396999	Finland, Stenroos 5595 (TUR)
<i>S. exutum</i>	KF644361	KY827017	Korea, Hur 130030 (KoLRI)
<i>S. exutum</i>	KF644362	KY827018	Korea, Hur 130031 (KoLRI)
<i>S. exutum</i>	DQ396948	DQ397022	Japan, Inoue 28958 (TUR)
<i>S. exutum</i>	DQ396950	DQ397024	Japan, Inoue 28953 (TUR)
<i>S. farinaceum</i>	DQ396973	DQ397049	Finland, Högnabba 382 (H)
<i>S. foliolosum</i>	DQ396933	DQ397008	China, Obermayer 8645 (GZU)
<i>S. foliolosum</i>	DQ396942	DQ397017	China, Obermayer 8644 (GZU)
<i>S. foliolosum</i>	DQ396951	DQ397025	China, Inoue 28949 (TUR)
<i>S. fronduliferum</i>	DQ396962	DQ397033	New Zealand, Vézda Lich. rar. exs. 279 (H)
<i>S. glabrum</i>	DQ396902	DQ396981	Argentina, Stenroos 5509 (TUR)
<i>S. glabrum</i>	DQ396906	DQ396985	Argentina, Stenroos 5460 (TUR)
<i>S. glareosum</i>	DQ396974	DQ397052	Finland, Högnabba 469 (H)
<i>S. intermedium</i>	DQ396934	DQ397009	China, Obermayer 8357 (GZU)
<i>S. intermedium</i>	DQ396946	DQ397020	China, Inoue 28948 (TUR)
<i>S. intermedium</i>	KF928151	KY827019	Korea, Hur 130044 (KoLRI)
<i>S. intermedium</i>	KF928152	KY827020	Korea, Hur 130055 (KoLRI)
<i>S. japonicum</i>	KY660024	KY827021	Korea, Hur 120706 (KoLRI)
<i>S. japonicum</i>	KF644365	KY827022	Korea, Hur 130069 (KoLRI)
<i>S. japonicum</i>	DQ396945	DQ397019	Korea, Inoue 28951 (TUR)
<i>S. myriocarpum</i>	DQ396931	DQ397006	China, Obermayer 8202 (GZU)
<i>S. myriocarpum</i>	DQ396954	DQ397028	China, Inoue 28950 (TUR)
<i>S. nanodes</i>	DQ396970	DQ397048	Norway, Løfall bpl-L 9587 (O)
<i>S. nigrum</i>	KF644367	KY827023	Korea, Hur 060664 (KoLRI)
<i>S. nigrum</i>	KF644368	KY827024	Korea, Hur 070924 (KoLRI)
<i>S. octomerellum</i>	KY660025	KY827025	Korea, Hur 121094 (KoLRI)
<i>S. octomerellum</i>	KP324748	KY827026	Korea, Hur 141479 (KoLRI)
<i>S. paschale</i>	DQ396897	DQ396977	Finland, Ahti 60905 (H)
<i>S. paschale</i>	DQ396924	DQ397001	Finland, Stenroos 5597 (TUR)
<i>S. pendulum</i>	DQ396969	DQ397041	Japan, Högnabba 247 (H)
<i>S. pileatum</i>	KP324749	KY827027	Korea, Hur 121815 (KoLRI)
<i>S. pileatum</i>	KF928154	KY827028	Korea, Hur 121822 (KoLRI)
<i>S. ramulosum</i>	DQ396944	DQ099629	Hawaii, Inoue 27242 (TUR)
<i>S. rivulorum</i>	DQ396967	DQ397038	Norway, Sipman 22112 (B)
<i>S. sasakii</i>	DQ369657	DQ397030	Japan, Sasaki 13823 (TUR)
<i>S. sasakii</i>	DQ369658	DQ397031	Japan, Sasaki 13825 (TUR)
<i>S. saxatile</i>	DQ396918	DQ396996	Finland, Stenroos 5591 (TUR)
<i>S. saxatile</i>	DQ396920	DQ396997	Finland, Stenroos 5594 (TUR)
<i>S. saxatile</i>	DQ396923	DQ397000	Finland, Stenroos 5596 (TUR)
<i>S. saxatile</i>	DQ396927	DQ397004	Finland, Stenroos 5603 (TUR)
<i>S. saxatile</i>	DQ396928	DQ397005	Finland, Stenroos 5606 (TUR)
<i>S. sorediiferum</i>	KF928155	KY827029	Korea, Hur 130032 (KoLRI)
<i>S. sorediiferum</i>	KF928156	KY827030	Korea, Hur 130046 (KoLRI)
<i>S. taeniarium</i>	DQ396919	DQ397053	Finland, Stenroos 5593 (TUR)
<i>S. tomentosum</i>	DQ396894	DQ099631	Finland, Ahti 60910 (H)
<i>S. tomentosum</i>	DQ396921	DQ396998	Finland, Stenroos 5607 (TUR)
<i>S. tornense</i>	DQ396975	DQ099632	Norway, Dahlkild s. n. (H)
<i>S. urceolatum</i>	DQ396959	DQ099624	Sweden, Muhr s. n. (TUR)
<i>S. verruciferum</i>	DQ396899	DQ099633	Argentina, Stenroos 5289 (TUR)
<i>S. verruculigerum</i>	KP324750	KY827031	Korea, Hur 130015 (KoLRI)
<i>S. verruculigerum</i>	KF644373	KY827032	Korea, Hur 130016 (KoLRI)
<i>S. verruculigerum</i>	DQ396930	DQ099634	Indonesia, Surdiman s. n. (TUR)
<i>S. vesuvianum</i> var. <i>nodosum</i>	KF644374	KY827033	Korea, Hur 090157 (KoLRI)
<i>S. vesuvianum</i> var. <i>nodosum</i>	KF644375	KY827034	Korea, Hur 130038 (KoLRI)
<i>S. vesuvianum</i>	DQ396925	DQ397045	Finland, Stenroos 5599 (TUR)

^aAbbreviation of herbarium name: Botanischer Garten und Botanisches Museum Berlin-Dahlem, Zentraleinrichtung der Freien Universität Berlin (B); Biozentrum Klein-Flottbek, Universität Hamburg (HBG); Karl-Franzens-Universität Graz (GZU); Korean Lichen Research Institute (KoLRI); University of Helsinki (H); University of Turku (TUR).

^bThe bold font indicates the 20 representatives from the 10 *Stereocaulon* species used in this study.

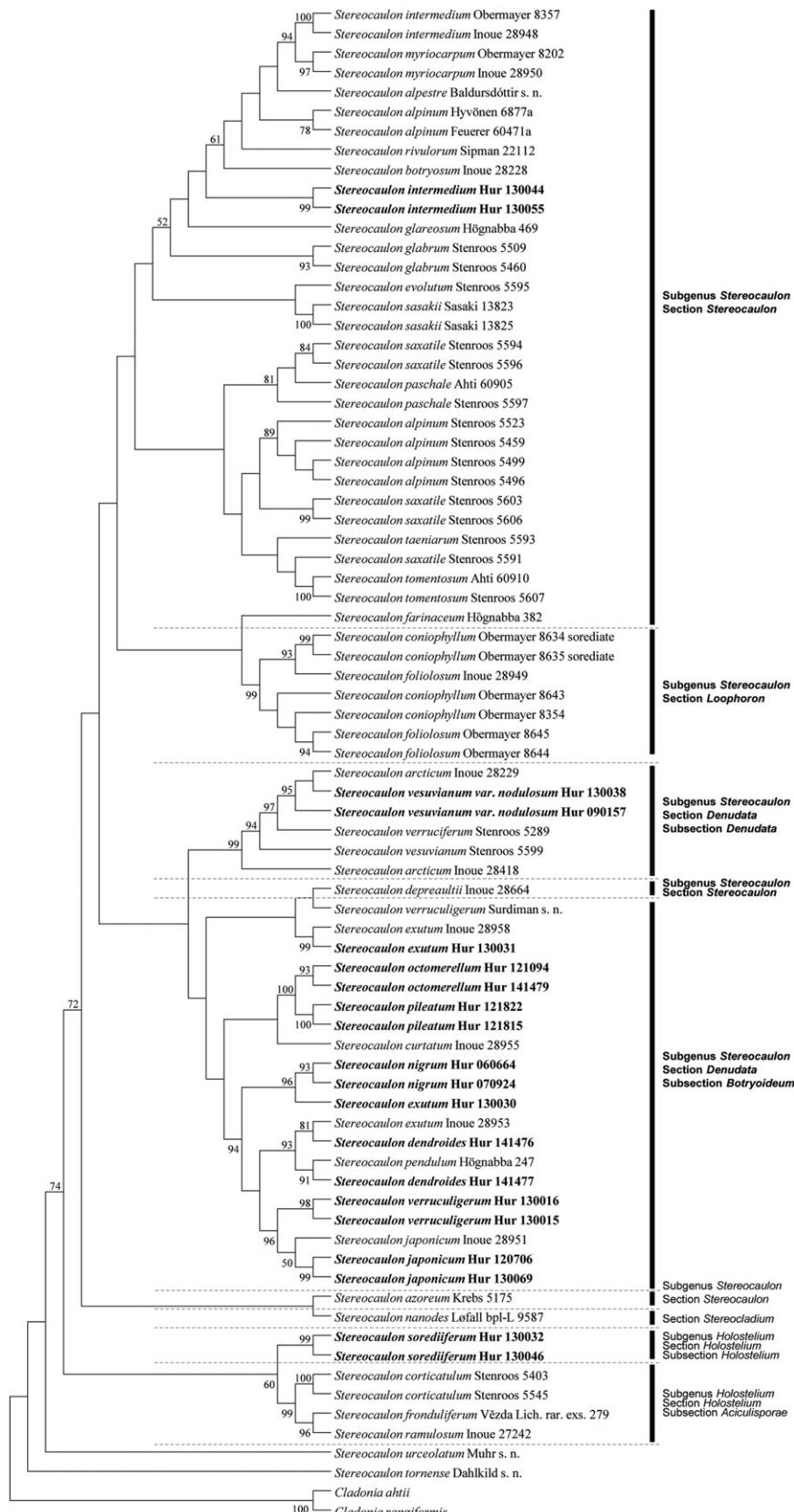


Figure 4. Maximum parsimony (MP) tree was constructed by MEGA6. The phylogenetic tree generated from internal transcribed spacer (ITS) sequences and part of the β -tubulin gene sequence. The bold letters in black indicate 20 representatives from 10 *Stereocaulon* species used in this study. Bootstrap = 1000. The numbers at each node represent bootstrap values. Only nodes supported by 50 bootstraps or more are shown.

value, which suggests that this “species” may be polyphyletic. It could be possible that the genetic sequence variation of the species may result from regional or morphological variation [11].

In conclusion, molecular analysis carried out in this study indicated that the molecular phylogeny of genus *Stereocaulon* in South Korea is largely in agreement with the previous molecular classification, except for *S. intermedium*. *S. intermedium* was not in accordance with previous findings [4]. This might have resulted from differences in the regional distribution of the specimens used in the previous study.

In this survey, we extensively collected specimens of the genus *Stereocaulon* in South Korea and identified them by morphological, chemical, and molecular analyses. This study will contribute and supplement further studies on lichen classification and ecology.

An updated taxonomic key to the lichen genus *Stereocaulon* in South Korea.

1. Soredia present 2
- Soredia absent 3
2. Pseudopodetia up to 1 cm *S. pileatum*
- Pseudopodetia over 1 cm *S. sorediiferum*
3. Phyllocladia spatulas apical foliar expansion at the ends of the pseudopodetia
..... *S. apocalypticum*
- Not above 4
4. PD + red (stictic acid present) 5
- PD- pale yellow (lobaric, porphyritic acid present) 8
5. Phyllocladia coralloid 6
- Phyllocladia peltate, foliose 7
6. Miriquidic acid present *S. commixtum*
- Miriquidic acid absent *S. japonicum*
7. Phyllocladia peltate
..... *S. vesuvianum* var. *nodosum*
- Phyllocladia foliose *S. wrightii*
8. Primary thallus persist 9
- Primary thallus lacking 11
9. Spore broad, 6–7(–9) µm, miriquidic acid present *S. curtatum*
- Spore narrow, not over 5 µm, miriquidic acid absent, lobaric acid present 10
10. Pseudopodetia up to 1 cm *S. octomerellum*
- Pseudopodetia over 1 cm, lobaric acid present, morphologically similar to *S. japonicum*
..... *S. verruculigerum*
11. Tomentum present 12
- Tomentum absent 13
12. Phyllocladia granular, cephalodia scabrid, blackish *S. paschale*
- Phyllocladia granular to terete coralloid, cephalodia spherical, gray *S. intermedium*
13. Lobaric acid present 14
- Porphyritic acid present *S. dendroides*

14. Spore up to seven septate, phyllocladia not over 2 mm long *S. octomerum*
- Spore usually not over five septate, phyllocladia over 3 mm long 15
15. Hypothecium colorless *S. exutum*
- Hypothecium brown *S. nigrum*

4. Description of the species

4.1. *Stereocaulon dendroides* Asahina, J. Jap. Bot. 36: 231 (1961)

Morphology: Primary thallus lacking; pseudopodetia dorsiventral, tuft-like, well-branched from the base, thinner toward the top, 3–4.5(–5) cm tall, rust red near the base, ligneous, slightly striate, glabrous, firmly attached to the substrate and attached by one holdfast, phyllocladia coralloid, cylindrical, thin, simple to branched, up to 1–1.5 mm long, densely distributed on the pseudopodetia, cephalodia conspicuous, gray, spherical, tubercular, 0.5–0.7 mm wide, present in the lower part of pseudopodetia. Apothecia terminal, convex, botryose-like, reddish brown, 0.8–1 mm wide, rare, epiphymenium pale brown, hymenium hyaline, 30–37.5 µm high, hypothecium brown, 100–150 µm high; spore fusiform, hyaline, 3–5 septate, 20–25 × 2.5–5 µm.

Chemistry: K+ yellow, P+ pale yellow. TLC: atranorin, porphyritic acid.

Remark: *S. dendroides* has unique secondary metabolites compared to other species. This species is close to *S. verruculigerum* but it has lobaric acid instead of porphyritic acid.

Representative specimen examined: Jeju-do, Jeju-si, Mt. Halla, alt. 1,658 m, on rock, 33°21'49.09"N, 126°30'42.3"E, 04 July 2012, S. Y. Kondratyuk, L. Lokös, S.-O. Oh, S. Joshi, J.-S. Hur, Hur 121345 (KoLRI 016388).

4.2. *Stereocaulon exutum* Nyl., Lichenes Japoniae: 18 (1890)

Morphology: Primary thallus lacking; pseudopodetia erect, dorsiventral, tapered, well-branched, 2.5–3.5 cm tall, mostly dichotomous, main branches rather thick, glabrous, exposing gelatinous layer, densely phyllocladiate, phyllocladia numerous, cylindrical-coralloid, thin, simple to delicately branched, dichotomously ramulose, up to 2–3 mm long, cephalodia gray, spherical to botryose, tubercular, 0.5–0.8 mm wide, mostly present in the lower part of pseudopodetia. Apothecia not common, terminal, convex, reddish brown to brown, 1–1.5 mm wide, epiphymenium brown, 17–25 µm high, hymenium hyaline, 37.5–50 µm high, hypothecium hyaline, 45–50 µm high; spores not observed.

Chemistry: K+ yellow, P+ pale yellow. TLC: atranorin, lobaric acid.

Remarks: *S. exutum* is similar to *S. nigrum*, but has colorless hypothecium in the apothecia. This species is characterized by containing lobaric acid and having longer and thinner phyllocladia, which are well-developed than in other species.

Representative specimen examined: Gangwon-do, Inje-gun, Mt. Sorak, alt. 660 m, on rock, 38°09'37.07"N, 128°19'26.05"E, 15 May 2005, J.-S. Hur, Hur 050254 (KoLRI 003158).

4.3. *Stereocaulon japonicum* Th. Fr., *De Stereocaulis et Pilophoris commentatio: Uppsala: 18 (1857)*

Morphology: Primary thallus persistent or soon evanescent; pseudopodetia erect, dorsiventral, 1–2 cm tall, upper part dichotomously branched, main stems 1 mm wide, glabrous, completely decorticated, firmly attached to the substrate, phyllocladia abundant, granular-like to cylindrical-coralloid, simple to branched, gray to dark green, up to 2 mm long, cephalodia common, spherical, tubercular, gray to brown, 0.5–1 mm wide, mostly present on the basal part. Apothecia mostly terminal or rarely lateral on branch, reddish brown to black, convex, 1–2 mm wide, immature apothecia have exiple, which disappear when mature, epihymenium brown, 20–30 µm high, hymenium hyaline, 50–100 µm high, hypothecium brown, 90–100 µm high; spore fusiform, hyaline, 3–5(–7) septate, 30 × 2.5–5 µm.

Chemistry: K+ yellow, P+ red. TLC: atranorin, norstictic, stictic, cryptostictic, menegazziaic, and constictic acids.

Remarks: *S. japonicum* is similar to *S. commixtum* but the latter has miriquidic acid and pseudopodetia are taller than that of *S. japonicum*. This species is also morphologically close to *S. verruculigerum* but differs in having stictic acid instead of lobaric acid. *S. japonicum* has much variation and is widely distributed in South Korea.

Representative specimens examined: Gyeongsangnam-do, Peak Ungseokbong, alt. 848 m, on rock, 35°22'58.08"N, 127°51'29.01"E, 16 October 2007, J.-S. Hur, Hur 070900 (KoLRI 007710); Gangwon-do, Mt. Hwangbyeong, alt. 772 m, on rock, 37°44'47.06"N, 128°37'31.05"E, 14 Jul 2008, Hur 080414 (KoLRI 008661); Jeollanam-do, Yeosu-si, Bulga coast, alt. 12 m, on rock, 34°39'00.04"N, 127°34'04.07"E, 28 April 2012, U. Jayalal, J. S. Park, J.-A. Rye, Hur 120706 (KoLRI 017060).

4.4. *Stereocaulon intermedium* (Sav.) Magn., *Bot. Mater. Inst. Sporov. Rast. Glavn. Bot. Sada RSFSR 2(11) 163. 1923: 163 (1923)*

Morphology: Primary thallus lacking; pseudopodetia erect, dorsiventral, caespitose, well branched from

the base to the top, becoming gradually thinner toward the top. 2.5–3.7 cm tall, 0.5–0.7 mm wide, decorticate, exposing inner layer, not ligneous, glabrous to thin tomentum, firmly attached to the rock, phyllocladia abundant, granular to verrucose in upper part, whereas in basal part terete to coralloid, partly squamulose-like, grayish white to white, 0.5–1 mm long, 0.1–0.2 mm wide, cephalodia abundant, sessile on pseudopodetia, violet-gray to brownish, spherical to botryose, tubercular, 1–2 mm wide, concealed in phyllocladia to conspicuous well on pseudopodetia. Apothecia are not observed.

Chemistry: K+ yellow, P- pale yellow. TLC: atranorin, lobaric acid.

Remarks: This species may be confused with other coraloid type species. According to Park, it is close to *S. verruculigerum* but differs by having a short tomentum and shorter pseudopodetia and is more whitish with verrucose phyllocladia at the young stage [11].

Representative specimen examined: Jeju-do, Jeju-si, Mt. Halla, alt. 1585 m, on rock, 33°22'04.03"N, 126°30'35.09"E, 04 April 2013, S.-O. Oh, J. S. Park, 130055 (KoLRI 018041); the same locality, alt. 1671 m, on rock, 33°21'35.01"N, 126°30'42.30"E, 02 May 2014, S.-O. Oh & J. S. Park, Hur 140098 (KoLRI 021271).

4.5. *Stereocaulon nigrum* Hue, *Nouv. Arch. Mus. Hist. Nat. ser. 3, 10: 248 (sep. 36) (1898)*

Morphology: Primary thallus lacking; pseudopodetia 2–4 cm tall, dorsiventral, tuft, well-branched, densely phyllocladiate, decorticate, exposing inner brownish layer, phyllocladia lateral, coralloid, cylindrical, simple to delicately branched, up to 2–3 mm long, cephalodia abundant, spherical to botryose, tubercular, dark gray, 1 mm wide. Apothecia terminal, convex, dark brown to black, epihymenium and hypothecium brown, hymenium hyaline; spores not observed.

Chemistry: K+ yellow, P+ pale yellow. TLC: atranorin, lobaric acid.

Remarks: This species is similar to *S. exutum* but differs in having pigmented brown hypothecium. Hypothecium color is the most important key for identification between *S. nigrum* and *S. exutum*.

Representative specimens examined: Gyeongsangbuk-do, Danyang-gun, Mt. Sobek, alt. 1325 m, on rock, 36°57'18.00"N, 128°28'52.03"E, 03 October 2003, J.-S. Hur, Hur 030817 (KoLRI 000608); Jeollanam-do, Sancheong-gun, Mt. Jiri, alt. 1346 m, on rock, 35°19'25.02"N, 127°44'25.04"E, 16 September 2006, J.-S. Hur, Hur 060664 (KoLRI 005038).

4.6. *Stereocaulon octomerellum* Müll. Arg., Jap. Bot. 45(3): 68 (1970)

Morphology: Primary thallus persistent consisting of coarse granules; pseudopodetia 0.5–1 cm tall, erect, not dorsiventral, rarely branched, decorticate, exposing layer, firmly attached the substrate, growing on rock, phyllocladia abundant, lateral, short coralloid to granule-like, 0.1–0.5 mm long, grayish white to gray, cephalodia spherical, tubercular, gray, distributed in the basal part. Apothecia abundant, terminal, convex, brown, 1–2 mm wide, epihymenium brown, hymenium brown, 60–70 µm high, hypothecium hyaline 70–75 µm high; spore fusiform, hyaline, mostly 3–7 septate (Figure 3(L)), rarely 9–10 septate, 25–53 × 5–6 µm.

Chemistry: K+ yellow, P- pale yellow. TLC: atranorin, lobaric acid.

Remarks: This is the first record of the presence of *S. octomerellum* in South Korea. This species is similar to *S. curtatum*, but the latter produces miriquidic acid. Most of coraloid group cannot be easily distinguished. Immature *S. verruculigerum* can be easily confused with *S. octomerellum*. *S. octomerellum* is more erect than *S. verruculigerum*, has short pseudopodetia (up to 1 cm), and hypothecium is almost colorless to pale brown but *S. verruculigerum* has brown hypothecium.

Representative specimen examined: Jeju-do, Jeju-si, Mt. Halla, alt. 1446 m, on rock, 33°22'21.09"N, 126°30'10.03"E, 04 April 2013, S.-O. Oh, J. S. Park, Hur 130063 (KoLRI 018049); the same locality, alt. 1630 m, on rock, 33°21'49.09"N, 126°30'52.06"E, 08 November 2014, J. S. Park, J.-J. Woo, D. Liu, Hur 141479 (KoLRI 032152).

4.7. *Stereocaulon pileatum* Ach., Lich. Univ.: 1–696 (1810)

Morphology: Primary thallus persistent consisting of wart-like, pseudopodetia erect, not dorsiventral, rarely branched, 1–4 mm tall, short and stubby, decorticate, attached directly to rock, phyllocladia granular to wart-like, short, soredia at tip of pseudopodetia, apical, capitate and powder-like, sometimes apothecia with soredia, cephalodia spherical, granular to tubercular, gray to violet, 0.5–1 mm diam., small, interspersed basal part on pseudopodetia. Apothecia rare, terminal, 0.2–0.5 mm wide, brown, subglobe to oval, epihymenium brown, 10–15 µm high, hymenium hyaline, 50–60 µm high, hypothecium brown, 40–50 µm high; spore hyaline, 3–4 septate, 23–26 × 3–4 µm.

Chemistry: K+ yellow, P-pale yellow. TLC: atranorin, lobaric acid.

Remarks: *S. pileatum* is a very tiny species that is closely related to *S. octomerellum* but differs in having capitate soredia tip of pseudopodetia.

Representative specimens examined: Gyeongsangnam-do, Geoje-si, Mt. Geumwon, alt. 1313 m, on rock, 35°43'07.70"N, 127°45'08.26"E, 25 May 2010, X. Y. Wang, H. S. Jeon & G. S. Han, Hur 100545; Jeju-do, Jeju-si, Mt. Halla, alt. 1670 m, on rock, 33°21'15.69"N, 126°31'46.43"E, 04 Jul 2012, S. Y. Kondratyuk, L. Lokös, S.-O. Oh, S. Joshi, Hur 121822 (KoLRI 016759).

4.8. *Stereocaulon sorediiferum* Hue, Nouv. Arch. Mus. Hist. Nat. ser. 3, 10: 250 (sep. 38) (1898)

Morphology: Primary thallus lacking, pseudopodetia erect, not dorsiventral, well-branched, 0.8–4 cm tall, grayish, corticated, main stems rather thick, attached directly to rock, phyllocladia lateral, well-branched, coraloid, 2–2.5 mm, soredia distributed at tip of branch, capitate, powder-like, whitish, cephalodia conspicuous, common, sacculate (sack-like), gray to dark gray. Apothecia not observed.

Chemistry: K+ yellow, P-Pale yellow. TLC: atranorin, lobaric acid.

Remarks: *S. sorediiferum* is characterized by sack-like cephalodia and soredia at the tip of phyllocladia and long pseudopodetia. *S. meyeri* is a similar species but has perlatolic acid instead of lobaric acid. *S. pileatum* also has soredia but is differently located at the tip of pseudopodetia.

Representative specimen examined: Gangwon-do, Inje-gun, Temple Beakdam, alt. 465 m, on rock, 38°10'25.08"N, 128°22'21.06"E, 11 October 2004, J.-S. Hur, Hur 041554; Jeju-do, Jeju-si, Mt. Halla, alt. 1313 m, on rock, 33°21'13.00"N, 126°29'51.03"E, 04 April 2013, S.-O. Oh, J. S. Park, Hur 130032 (KoLRI 018017).

4.9. *Stereocaulon verruculigerum* Hue, J. Hattori bot. Lab. 43: 267 (1977)

Morphology: Primary thallus persistent as wart-like; pseudopodetia erect, 1–2 cm tall, dorsiventral, decorticate, exposing inner layer, little branched but becoming well-branched toward apices, densely phyllocladiate, phyllocladia abundant, coraloid, cylindrical, simple to branched, up to 1–2 mm long, cephalodia common, mostly located on basal part, spherical, tubercular, gray to black, 0.5–2 mm wide. Apothecia terminal, convex, reddish brown to black, 1–2 mm wide, abundant, epihymenium brown, 50–100 µm high, hymenium hyaline, 50–100 µm high, hypothecium brown, 50–100 µm high; spore fusiform, hyaline, 3–4(–6) septate, 25–50 × 2.5–5 µm.

Chemistry: K+ yellow, P-pale yellow. TLC: atranorin, lobaric acid.

Remarks: This species is very similar to *S. japonicum*, but contains stictic acid instead of lobaric acid. *S. octomerellum* is also a similar species but has short pseudopodetia (up to 1 cm long). According to the Lamb key, *S. verruculigerum* has a primary thallus but according to the Japanese key it does not [6]. “The Macrolichen flora of South Korea” states that this species has a primary thallus [11]. It is very difficult to distinguish these species from *S. japonicum* without a TLC test.

Representative specimen examined: Jeollabuk-do, Muju-gun, Mt. Deokyu, alt. 1550 m, on rock, 35°50'22.04"N, 127°44'48.00"E, 30 April 2005, J.-S. Hur, Hur 050185 (KoLRI 003088); Gyeongsangbuk-do, Yeongju-si, Mt. Sobeak, alt. 1270 m, on rock, 36°57'19.08"N, 128°09'17.00"E, 30 Mar 2013, U. Jayalal, J. S. Park, Hur 130015 (KoLRI 018000).

4.10. *Stereocaulon vesuvianum* var. *nodosum* (Wallr.) I.M. Lamb, Best. europ. Flecht. (Vaduz): 633 (1969)

Morphology: Primary thallus lacking, pseudopodetia decumbent, well-branched, 1.5–2.5 cm tall, decorticate, brown exposing layer, woody, twisted, main stem rather thick and robust than other branches, 1–1.5 mm wide, densely phyllocladiate, firmly attached on the rock, phyllocladia peltate with dark center (greenish gray) and pale margin (grayish white to whitish), 0.5–1 mm wide, at first convex then flattened and finally developing a depressed, slightly tumid, squamulose-like, cephalodia not seen. Apothecia terminal to lateral, brown to black, 0.5–1 mm wide, convex, epiphyllum brown, 12–12.5 µm high, hymenium and hypothecium hyaline to brownish; spore hyaline, 12.5 × 2.5 µm, no septate.

Chemistry: K + yellow, P + red. TLC: atranorin, norstictic acid, stictic acid, cryptostictic acid, menegazziaic acid, and constictic acid.

Remarks: This species has peltate phyllocladia and can be easier to separate than others. This species appear near a volcano in South Korea and has many variations.

Representative specimens examined: Jeju-do, Jeju-si, Mt. Halla, alt. 1547 m, on rock, 33°22'06.09"N, 126°30'32.09"E, 04 April 2013, S.-O. Oh, J. S. Park, Hur 130060 (KoLRI 018046); Jeollanam-do, Mt. Baekun, 915 m, 35°04'09.06" N, 127°39'24.04"E, 25 September 2004, J.-S. Hur, Hur 041296.

4.11. Species excluded from this study

According to the literature, the species of *S. apocalypticum* Nyl., *S. commixtum* (Asahina) Asahina, *S. curtatum* Nyl., *S. octomerum* Müll. Arg., *S. paschale*

(L.) Hoffm., and *S. wrightii* Tuck. have been reported in Korea. However, this time we did not detect these species. We have descriptions based on previous literature.

4.11.1. *Stereocaulon apocalypticum* Nyl., in Middendorff, Reise Sibir. 4(6): LV (1867)

This species is characterized by phyllocladia. Phyllocladia represented by spatulate apical foliar expansions at the end of the pseudopodetia [6]. It has a very distinct phyllocladia form which can be easily characterized in the field. It has previously been reported by Kim [10] and has also been found in China [30] and Japan [13].

4.11.2. *Stereocaulon commixtum* (Asahina) Asahina, (1969)

This species is characterized by having miriquidic acid, densely coraloid phyllocladia and tubercular cephalodia gray to blackish. It closely resembles *S. japonicum*. Both species have stictic acid, but *S. commixtum* additionally produces miriquidic acid. *S. verruculigerum* is also morphologically similar, but *S. verruculigerum* has lobaric acid instead of stictic acid. Although the three aforementioned species are morphologically very similar, they can be distinguished using the TLC method. *S. commixtum* has been reported by Park in Korea [11] and has also been found in Japan [13].

4.11.3. *Stereocaulon curtatum* Nyl., Lich. Japon.: 18 (1890)

This species is characterized by having coraloid phyllocladia, broad spore size (6–9 µm) and contains miriquidic acid. It is similar to *S. octomerellum* but the latter has a grain-like or verruculose phyllocladia and contains lobaric acid instead of miriquidic acid. This species has been reported by Kim [10] and it has been also found in Japan [13].

4.11.4. *Stereocaulon octomerum* Müll. Arg., Flora, Regensburg 74(1): 109 (1891)

This species is characterized by evanescent primary thallus, presence of minutely granule-like to short coraloid phyllocladia and usually seven septate spores. This species is also very similar to other coraloid type *Stereocaulon*, but it has seven septate spores, whereas the other species have three to five septate spores. This species has been reported by Park [11] and has also been found in Alaska [31], Japan [13], and Taiwan [32].

4.11.5. *Stereocaulon paschale* (L.) Hoffm., *Deutschl. Fl., Zweiter Theil (Erlangen): 130 (1796)* [1795]

This species is characterized by having scabrid cephalodia, verrucose to digitate-squamulose phyllocladia, and thinly tomentum. It is a cosmopolitan species, widely distributed in the American arctic [33], Finland [34], North America [35], Patagonia [36], Canada [2], and British Isles [37]. In East Asia, it has been found in China [27] and Japan [13].

4.11.6. *Stereocaulon wrightii* Tuck., *Amer. J. Sci. Arts, Ser. 2 28: 202 (1859)*

This species is similar to *S. apocalypticum* but is distinguished by the presence of stictic acid instead of lobaric acid. It is characterized by the presence of pseudopodetia 1 to 4cm, solitary or caespitose, branched above, apical foliar expansions of phyllocladia and cephalodia doubtful [38]. It has reported by Sato [9] and Kim [10] and in East Asia, and has been found in Japan [13].

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Disclosure statement

No potential conflict of interest was reported by the authors.

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